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Review and synthesis

A cross-scale framework to support a mechanistic understanding and modelling of marine climate-driven species redistribution, from individuals to communities

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Climate-driven species redistribution is pervasive and accelerating, yet the complex mechanisms at play remain poorly understood. The implications of large-scale species redistribution for natural systems and human societies have resulted in a large number of studies exploring the effects on individual species and ecological communities worldwide. Whilst many studies have investigated discrete components of species redistribution, the integration required for a more complete mechanistic understanding is lacking. In this paper, we provide a framework for synthesising approaches to more robustly understand and predict marine species redistributions. We conceptualise the stages and processes involved in climate-driven species redistribution at increasing levels of biological organisation, and synthesize the laboratory, field and modelling approaches used to study redistribution related processes at individual, population and community levels. We then summarise links between scales of biological organisation and methodological approaches in a hierarchical framework that represents an integrated mechanistic assessment of climate-driven species redistributions. In a rapidly expanding field of research, this framework provides direction for: 1) guiding future research, 2) highlighting key knowledge gaps, 3) fostering data exchange and collaboration between disciplines and 4) improving shared capacity to predict and therefore, inform the proactive management of climate impacts on natural systems.

Keywords: climate change, integrative ecology, interdisciplinary approaches, macroecology, marine species redistribution, mechanistic models



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Introduction

Climate-driven species redistribution (or range shift) science is a rapidly emerging field that connects multiple established disciplines, including trophic ecology, thermal ecology, evolutionary biology, population genetics and physiology (Bonebrake et al. 2018). Extensive climate-driven shifts in marine ectotherms' distributions across latitudes and with depth have been widely documented (Dulvy et al. 2008, Sorte et al. 2010, Poloczanska et al. 2013) and are linked to major implications for ecosystem services and human well-being (Rosenzweig et al. 2008, Pecl et al. 2017). Species redistribution science aims to enhance predictive capacity of future changes and inform appropriate climate adaptation strategies, and is challenged with the task of elucidating the mechanisms underlying observed ecological responses to contemporary climate change (Bonebrake et al. 2018). However, whilst used widely, the limitations of applying trait-based, taxonomic and geographical methods for understanding and predicting climate-driven range shifts remain a challenge (Lenoir and Svenning 2015). An integrated framework, that is tailored to achieve a mechanistic understanding of species redistributions, is required to effectively address this challenge. Such a framework, which can synthesise different methodological approaches across varying scales of biological organisation, is presently lacking, thus hampering the practical applicability and cross-disciplinary communication of species redistribution research.

Species redistribution is a global phenomenon and is now commonly occurring as a result of climatic change (Parmesan and Yohe 2003, Poloczanska et al. 2013, 2016). Here, we define a species range shift as 'a change in the distribution of native species' geographical boundaries from their previously recorded boundaries', which occurs through expansions and/or contractions of the range edges (Madin et al. 2012, Bates et al. 2014). Range shifts are diverse in speed and distance due to interplay with various other factors, such as the velocity of climate change (Burrows et al. 2011, Sunday et al. 2015, García Molinos et al. 2016), species phenological shifts (Socolar et al. 2017) and local population adaptations (Moran et al. 2016). Range shifts are pervasive; studies investigating communities and assemblages have found that 20–85% of species are shifting in response to climate change (Dulvy et al. 2008, Chen et al. 2011, Wernberg et al. 2011). Evidence shows that marine species are shifting an order of magnitude faster than terrestrial species (Poloczanska et al. 2013). This faster rate of species shifts in marine systems suggests that an examination of marine species redistributions may be potentially informative in attempting to resolve causal mechanisms. Moreover, these rapid and extensive species redistributions place the marine environment, and the associated human livelihoods, at greater risk (Pecl et al. 2017).

Species range shifts can have positive and/or negative effects on human health, culture, economies and ecosystem services (Madin et al. 2012). Therefore, an improvement in current predictive capacity is important for researchers and

marine managers, as well as resource users. Species distributions can be shaped by biotic interactions at, and beyond, local areas (Wisz et al. 2013) and exhibit naturally dynamic range edges, which challenge our predictive capacity for species movements (Bates et al. 2014). Confidence in separating true range shifts from sampling artefacts may be achieved by coalescing modelling approaches to explore empirical data (Bates et al. 2015). These modelling approaches use a wide array of methods and data types. As a result, selecting the most appropriate method for the data available requires increased knowledge of the mechanisms at play (Elith and Graham 2009), which itself presents limitations and uncertainties when using data unique to a particular space and time, or of a novel environment (Dormann et al. 2013, Briscoe et al. 2016).

The influence of environmental variables on species redistribution has largely overshadowed the intrinsic effect of biotic interactions on species range shifts. There is no doubt biotic interactions can influence local species presence and abundances; yet few studies investigate how these interactions could influence range shifts under climate change scenarios. The development of predictive tools that can better incorporate these biotic interactions into range shift forecasts are necessary to explore and understand their importance during climate change-induced species redistribution (HilleRisLambers et al. 2013). Further, combining relevant research approaches to inform the selection of research methods and data types can also encourage the adoption of new research methods and approaches (Elith and Graham 2009).

The ability to effectively manage marine resources under a changing climate relies on furthering understanding of the mechanisms underlying species redistributions. Species distribution models (SDMs) that establish correlative links between environmental conditions and species distributions are widely used (Thomas et al. 2004, Guisan and Thuiller 2005, Elith and Leathwick 2009), and have been instrumental in furthering the field of conservation planning. However, species redistribution analyses, particularly in marine systems, remain commonly informed by correlative SDMs (Champion et al. 2018) that do not incorporate mechanistic relationships between species and their environments and are thus susceptible to producing inaccurate predictions under novel environmental and ecological scenarios (Sinclair et al. 2010). Recent advances in the development of hybrid SDMs that incorporate correlative and process-based methods are providing increasingly detailed forecasts of climate-driven species redistribution by incorporating, for example, population dynamics (Dullinger et al. 2012) and evolutionary processes (Bush et al. 2016). To date, these methodological advances have primarily focused on terrestrial systems and a greater incorporation of mechanistic responses into marine SDMs is now required to better assess biological responses to rapidly changing marine environments (Hobday and Pecl 2014). A major advantage of mechanism-based analyses is the establishment of causal relationships that can inform predictions of species distributions and investigations of species potential

for redistribution (Connolly et al. 2017). Mechanistic models focus on parameters with direct biological interpretation and therefore provide meaningful understanding of the causes of species redistribution, and potentially be applied as useful tools for investigation (Connolly et al. 2017). Here lies an opportunity to use mechanistic approaches to understand the functional role of different species' (e.g. Gérino et al. 2003) experiencing redistribution, and to allow related research to expand from simply assessing the redistribution of individual species to gaining a general understanding of the underlying ecological principles of range shifts.

In theory, mechanistic models should have a better capacity to predict unprecedented system shifts than purely statistical methods. Yet, species trait-based approaches have had mixed success in understanding species redistributions (Angert et al. 2011, Sunday et al. 2015, Estrada et al. 2016). A key challenge for mechanistic models is to identify the main mechanisms that determine abundance and dispersal, interactions with the environment and responses to climate change, and to describe these mechanisms in mathematical terms, e.g. linear or non-linear responses. This requires cross-disciplinary dialogue and collaboration to identify these key species traits and the processes that drive them, and develop mechanistic models that can include them in a dynamic framework (Buckley et al. 2010). However, current practices including limited communication and other barriers within and between research disciplines means that data and findings are not necessarily shared effectively, and theories shaping one discipline are often not seen as important in another. One example is the current debate on whether or not increased temperatures are likely to lead to oxygen limitation in ectotherms (Cheung et al. 2012, Lefevre et al. 2017, Pörtner et al. 2017, Jutfelt et al. 2018, Pauly and Cheung 2018, Audzijonyte et al. 2019) and the role that oxygen limitation will likely play in determining species range limits and species distributional responses to climate change. Another key uncertainty is related to whether short-term responses to temperature measured under laboratory conditions, such as smaller ectotherm adult body sizes in warmer conditions, can be extrapolated to predict intergenerational and long-term species responses in the wild (Donelson and Munday 2015, Audzijonyte et al. 2020).

The objective of this synthesis is to provide a hierarchical framework of methods, through which to explore the effects of climate-driven species redistribution from the individual level through to communities via the transfer of knowledge and approaches between different research fields. We explore a range of performance measures and provide several examples that incorporate some of these measures, highlighting the significant gaps and future modelling needs that should be addressed to better understand and predict future changes. By developing a list of physiological, biological and ecological measures, and their potential use in models, we hope to guide the integration of diverse disciplinary knowledge and improve understanding and predictive capability of how marine species may respond to climate change.

Methods and results

Species redistribution processes

To improve understanding and overcome barriers to integration, we developed a conceptual framework (Fig. 1 and Table 1) that connects different stages of species range shifts (adapted from Bates et al. 2014, but also see Lenoir and Svenning 2013) with the various processes operating at each scale of biological organisation. Stages of species range contractions are defined as persistence, performance decline, population decrease and local extinction, while stages of species range extensions are defined as absence, arrival, population increase and persistence (Fig. 1, x-axis). This conceptual framework was developed following a workshop and discussion of the processes relevant to species redistribution by a team of researchers working in a range of fields including physiology, biology, ecology and modelling. The outcome of the workshop resulted in expert knowledge on species redistribution processes that was collected and defined in a hierarchical, illustrated framework from individual to community level processes (Fig. 1). The figure identifies processes in five general categories: physiological capacities, behaviour and biotic interactions, plasticity and adaptation, reproduction and dispersal, and human interactions. These process categories were then divided into more detailed process capacities, e.g. physiological, aerobic and anaerobic, immune and neuro-physiologic, growth, energy and bioenergetics, and locomotor performance. The capacities were then characterised to affect species either directly or indirectly at different levels of biological organisation; individual, population or community. These processes can intersect and interact with each other and across levels of organisation in both directions. Data used at one stage may also be useful in other stages (Fig. 1).

The course and confidence of our knowledge in range extensions through arrival, increase and persistence of populations are mirrored by a contraction pathway indicating a decline in performance, decreases in population and ultimately local extinction (lower part of Fig. 1). Processes that relate to range contraction (extension) are arranged on the left (right) side of Fig. 1. Physiological capacities (purple) directly affect species at the individual level, and this cascades up to population and community levels through indirect effects, for example how an individual's aerobic capacity may affect its fecundity or recruitment or competitive interactions. On the other hand, community or population level characteristics such as density may reversely affect individual level traits, such as feeding rates, gregariousness or immune capacities (Fig. 1). If conditions for a species become more favourable in an area previously unsuitable to them, physiological capacities are likely to increase. From there, flow-on effects from increased physiological capacity may positively influence behaviours and biotic interactions, and reproduction and dispersal, leading to a range extension of the species. In contrast, the left-hand side of Fig. 1 can be used to identify

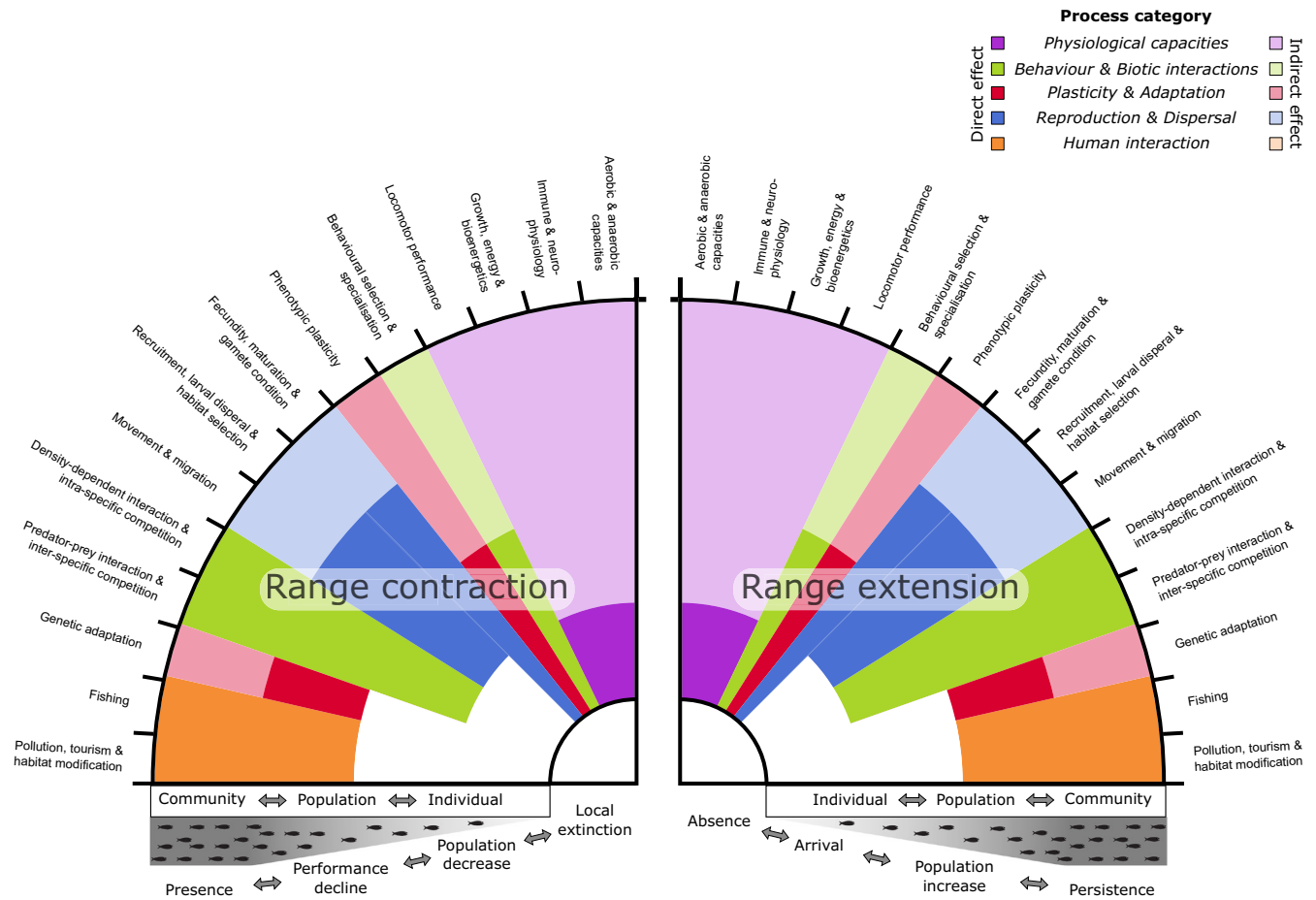


Figure 1. The processes associated with climate-driven species redistribution ecology are presented for both the range contraction (left) and range extension (right) pathways. Coloured wedges indicate categories of processes operating at various organisational levels (y-axis in the middle of the figure) and stages (x-axis) of a range shift. Within each coloured wedge, dark colours indicate the levels at which processes predominate, light colours indicate the indirect effects of the processes projected to higher levels, and white segments indicate no effect at the corresponding level. The bidirectional arrow indicates that organisational level characteristics may interact from individuals to community and vice versa.

processes related to species range contractions. As individual species' physiological performance starts to decline, flow-on effects to higher levels will lead to changes in population level processes, e.g. decreases in larval recruitment. Such top-down effects of environment on individual traits can be included in mechanistic models if processes can be clearly identified and described mathematically. Some species traits, such as growth rates, feeding level, realised predator-prey mass ratio, maturation age, reproductive output-at-age or recruitment, are already represented as emergent properties in many currently used physiologically structured models (Fig. 2). These traits will depend on individuals' interaction with its environment, which in turn will determine its success and abundance. Existing frameworks could generally include more environmental feedbacks on species traits, but the specification of these traits and their parameters relies on the effective cross-disciplinary communication and availability of data to assess performance of more complex models.

Tools to investigate redistribution processes

Based on the developed hierarchical framework, we identified relevant tools and methods for attaining the desired data required for the processes detailed in Fig. 1, as outlined in Table 1. From the process stage (e.g. aerobic and anaerobic capacity), nested measures of that process were identified via expert and literature review (e.g. metabolic rates, aerobic scope, Table 1). During the workshop, many of the measures and tools to investigate those measures were identified. Following the expert knowledge phase, gaps in either measurements or tools were filled by a literature search for relevant studies using the identified tools in a climate-range shift context. The literature review was conducted across two databases, Scopus and Web of Science. Search terms used were a combination between the identified process (e.g. aerobic capacity), measure (e.g. metabolic rates), and/or tool (e.g. respirometry) from Table 1, in combination with terms such

as ‘range shifts’ or ‘species redistribution’. When these terms did not produce a result, due to the lack of information for some of the measures and tools associated with species redistribution, ‘climate change’ or ‘ocean warming’ were added to the search. Where references not specific to species redistributions were found, if relevant to investigating an aspect of redistribution science (e.g. thermal biology), they were included as they were deemed useful in their potential to be used in species redistribution science in the future. Abstracts of all publications selected were read, and the ones deemed not suitable were discarded. The rest of the papers were read in full to ensure reference eligibility.

Table 1 presents a hierarchical framework providing researchers with a synthesis of approaches that can be used to aid in guiding future research. Our synthesis of methodological approaches integrates different levels of biological complexity and potential drivers of species redistribution. For different measures of species performance, we provide examples of suitable laboratory, field and modelling methods that can be used to understand how these measures are influenced by different factors (for example, temperature and pH) and how they are likely to affect species’ ecologies under climate change. Our framework identifies tools suited for investigating different measures of species performance over different levels of biological complexity, from individual level processes up to population and community levels. For example, competition experiments can provide metrics of competitive success under different climate change scenarios to infer how changes in the abiotic environment are likely to affect intraspecific competition. Importantly, the individual level processes presented in Table 1 are often nested within higher levels, recognising the increasingly complex nature of climate change at community level. The tools presented in Table 1 can be used individually, but as more measures of performance are investigated, the better the understanding (Twinn et al. 2019) and predictive capacity when they are incorporated into models.

Mechanistic modelling frameworks to predict species redistributions

Only a fraction of the processes listed in Table 1 have been explicitly or implicitly included into mechanistic redistribution models, but many more processes have been considered in various other individual, population and community physiologically structured models (Fig. 2 and Supplementary material Appendix 2 for the full literature list). Figure 2 lists some examples of individual, population and community-level models incorporating physiological processes, and the required data identified in Table 1. Individual models generally focus on individual performance, such as emergent growth, aerobic scope or reproduction under specific environmental conditions, and have been used to predict how changing conditions might affect a species’ performance and by inference, its success in a new community (Holt and Jørgensen 2015). Population level models include individual level mechanistic processes, but also allow for emergent

population level processes, including density dependence or evolution (Fig. 2). Finally, the full range of individual, population and community processes can be explicitly considered in community models, where species interactions can act on individual and population level dynamics. These community models can range from a subsection (e.g. MICE models), through to attempts at full representation of the ecosystem (e.g. Atlantis) (Plagányi et al. 2011, Pethybridge et al. 2019). Notably, some processes and mechanisms that are likely to be critical in range shifts, such as sensory physiology, immune capacity, phenotypic plasticity or genetic adaptation, remain largely ignored in widely used physiologically structured models (Fig. 2). However, these frameworks could be relatively easily expanded to include new mechanisms (e.g. temperature effects on baseline mortality to represent immune response), provided there is an agreement on their importance and ways to describe them mathematically.

Putting the framework pieces together

The aim of this paper is to facilitate the transfer of knowledge and approaches from different research areas to provide a better understanding of current and future species redistributions. By providing a framework that illustrates a range of processes, measures, tools and models, this integration of different disciplines might be easier to navigate. The need for this framework stems from a current lack of dialogue between researchers focussed on observations, and researchers focussed on models, that creates a disconnect that may lead to data and model projection inefficiencies (Fig. 3a). Figure 3 highlights this disconnect between researchers as well as the solution, including how to use this framework to investigate current and future species redistributions.

In very general terms, we can say that those involved in species distribution science could be separated into two main categories; those who are focussed on observations, and those focussed on modelling (acknowledging these categories are not clear cut). For example, a physiologist may examine a range-shifting species, collect the data on some potentially important physiological parameter and then try and make predictions about how the data might inform different processes. A modeller on the other hand might have a different approach, starting with the model that already includes main processes (often based on tradition and ease of modelling), and then try to find data that can be used to parameterise the model. These two approaches, in isolation, can lead to problems such as data not suitable for existing models or model data requirements that cannot be fulfilled. The solution to this problem is an early dialogue (Fig. 3b), where major processes are identified from the start, and data collection and model development are done in collaboration. Different perspectives can be shared on which processes are particularly relevant for species redistribution, in terms of ecological or physiological relevance, how these processes can be summarised mathematically and what data is required to parameterise and validate models.

Table 1. Synthesis of important ecological processes implicated in species redistribution ecology that align with key performance measures and methodological tools appropriate for their quantification. Ecological processes are partitioned into corresponding levels of biological organisation, where key performance measures and methodologies applicable at lower levels of organisation (i.e. individual level) are often also applicable to, and thus nested within, higher levels of organisation (i.e. community level). Supplementary material Appendix 1 provides the list of references for the associated process, measure or tool. Colour of process category indicates a match to Fig. 1.*

Level of organisation	Process category	Process	Measure	Tools
Individual	Physiological capacities	Aerobic capacity	Maximum and standard metabolic rates [1, 2] Aerobic scope [2] Critical thresholds [4] Oxygen extraction capacity Blood oxygen transport Heart rate, stroke volume [13] Mitochondrial capacity	Respirometry experiments [2] Respirometry experiments [1, 3] Temperature and oxygen ramping experiments [5, 6, 7, 8, 9] Cannulisation: ratio of surface areas, electrocardiography Haemoglobin/haematocrit analysis [10, 11], haemoglobin isoform analysis [12] Electrocardiography (experimental [14] or field [15]) High resolution respirometry [16], fluorophore-based measurements to measure ATP or membrane potential, electron microscopy to measure mitochondrial cristae density [17] Oxygen microensors, patch-clamp electrophysiology [15] Post-exercise respirometry experiments [18] Spectrophotometric enzyme analysis [19, 20, 21], RNA expression/transcriptomics [22] Differential cell counting [24] Immune challenge experiments [25, 26] RNA-sequencing [27], RNA sequencing, RT-qPCR [29], RNA-FISH [30] Visual acuity/Y-maze tests [32] Atena flume experiments [33, 34] Auditory choice chamber experiments [35] Otolith chronology [36], mark-recapture [37], experimental growth trials [38] Feed conversion experiments [39] Growth-feeding experiments [40, 41] Apparent digestibility coefficient [42] Serial-slaughter method [44, 45], inert markers Spectrophotofluorometric assays [42] Fed respirometry experiments [47] Omics [48], inhibitor and tracer experiments Correlation between empirical multi-trait data [50, 51] Swim tunnel sustained/burst swimming trial [52], spontaneous activity observations (for species that can't be induced to move fast) [53] Response stimulus experiments [54, 55] Respirometry (benthic) [56], swim tunnel respirometry [57] Righting response trial [53, 58] Muscle stimulation force transducer trial [59] Excitatory junction potential [60] Choice experiments (shuttle/choice tanks) [7, 62, 63, 64], field-based body temperature/O ₂ logging [65]
		Anaerobic capacity	Tissue oxygen diffusion, ionic current (myocytes) Excess post-exercise oxygen capacity (EPOC) Anaerobic enzyme activity	Lab and field-based choice experiments [66] Lab and field-based choice experiments [67] Aquaia or mesocosm videography [68], field or mesocosm accelerometer/electromyography/biologging/telemetry [69, 70] Field or mesocosm accelerometer/electromyography/biologging/telemetry-calibrated [72] Personality [73] Correlation structure of empirically/experimentally derived behavioural traits [74], correlation with environmental physiological sensitivity [75], mesocosm experiments [76] Incubation to target levels of physical parameters e.g. temperature, oxygen, pH, CO ₂ over varying time and parameter change magnitude [79] Incubation to target levels of physical parameters over developmental stages RNA sequencing [81] Gonadosomatic index, gamete counts, egg production trials [84] Macroscopic and histological examination of gonads across animal size spectrum [85] Macroscopic and histological examination of gonads across animal size spectrum across season [85] Microscopy [86] Hatching trials [84], fertilization trials pH sensitive dye [88] Video microscopy [89]
		Immune capacity	White blood cell counts [23] Phagocytotic capacity, antibody production Expression of immune system linked genes [27, 28]	
		Sensory physiology	Vision [31] Olfactory Auditory	
		Growth capacity	Growth rate Cost of growth	
		Bioenergetics	Feed intake rate Assimilation Gut evacuation rate [43] Digestive enzyme activity Specific dynamic action [46] Protein, carbohydrate and lipid metabolism Energy budgeting conflicts and life history trade-offs [49] Maximum speed/maximum sustained speed	
		Energy allocation		
		Locomotor performance		
	Behaviour	Behavioural selection/specialisation	Fast start response performance Cost of transport Return to equilibrium Force production Neuromuscular transmission [60] Environmental parameter (e.g. thermal and dissolved oxygen) preference [9, 61] Diet preference Habitat preference Spontaneous activity patterns and movement rate	
			Energy budget use/active metabolic rate [71] Personality Behavioural trade-offs, plasticity and pace of life syndromes [49] Change of physiological or behavioural measures (see above)	
		Phenotypic plasticity [77, 78]	Developmental plasticity [80] Qualitative change in gene expression Fecundity [83] Size at reproductive maturity Timing of reproductive maturity Egg size Egg viability Egg intracellular pH [87] Sperm motility	
		Reproductive output [82] Maturation dynamics		
Reproduction and dispersal	Reproduction and dispersal	Reproductive output [82] Maturation dynamics		
		Gamete condition		

(Continued)

Table 1. Continued

Level of organisation	Process category	Process	Measure	Tools
Population	Reproduction and dispersal	Recruitment	Larval recruitment	Field based recruitment monitoring, collectors and traps [90]
		Larval dispersal	Stock recruitment	Fisheries stock-recruitment models
			Dispersal distance	IBM dispersal models [91, 92]
			Dispersal envelope	IBM dispersal models
			Physiological survival	Field tracking of larvae [93, 94]
Community	Biotic interactions		Recruitment success	Field based recruitment monitoring
			Dispersal/movement rates/movement strategy	Field based animal tracking: satellite telemetry [95], acoustic telemetry [96], fisheries data series [97], mark-recapture studies [98]
		Habitat association/distribution and structure	Habitat affinity and selection indices	Bathymetry, video surveys, cue experiments [93]
			Habitat contiguity/connectivity [99, 100]	Landscape pattern metrics [101]
			Fine-scale habitat complexity/microrefugia availability [102, 103]	Habitat complexity metrics [104]
	Adaptation	Density-dependent interactions	Local-regional climate coupling [105]	Fine-scale remote sensing, microhabitat models [102]
			Feed preference, feed intake, feeding efficiency, cannibalism rate	Density-dependent feeding experiments [106]
			Habitat selection	Habitat selection metrics from occurrence (telemetry or video) data [107]
	Human interactions	Intraspecific competition	Depensation Allee effect [108]	Experiments on nearest partner distances [109, 110]
		Genetic adaptation	Metrics of competitive ability	Competitive experiments for food/shelter/mates
Community	Biotic interactions		Phenotypic variation [113]	Intra-range variability of individual process metrics
			Allele/genotype/epi-genotype frequencies [115]	Transgenerational breeding experiments [116, 117, 118, 119], genotyping [115, 120], RNA-sequencing [83, 112, 117, 121], luminometric methylation assay, bisulfite conversion and sequencing
		Commercial and recreational fishing	Exploitation rate/fisheries mortality [122]	Demographic models with fisheries [123], mark recapture data [124]
		Predator-prey interaction	Predation rate, attack and escape speeds	Predator-prey arena trial and videography [125], videography [126, 127]
			Food availability	Field based surveys of resources
	Human interactions	Interspecific competition	Feeding preferences and selectivity [128]	Choice experiments
		Commercial and recreational fishing	Trophic dynamics [129, 130, 131]	Stable and compound specific isotopes
			Metrics of competitive ability	Competitive experiments for food/shelter/mates [132, 133, 134]
			Niche overlap e.g. diet and habitat	Gut content analysis (see habitat analysis)
			Fisheries mortality of prey, competitors or predators [135]	Demographic models with fisheries [123], mark recapture data [124]
Community	Human interactions	Species introductions [136]	Species presence, facilitation [137], climate-alien species synergies [138]	Occupancy models [139], lab trials, historical data modelling
		Environmental management/modification	Species health, pollution, chemical load, tourism, marine protected area implementation [140], habitat fragmentation [100]	Bioaccumulation models [141], temperature-toxicity experiments [142, 143], socio-economic modelling [144], observational MPA experiments [145]

† There are many factors to be considered when determining which measure and tools to use when investigating the effect of climate change on species performance. Factors influencing individual level processes include abiotic factors, such as temperature, salinity, pH, light and oxygen levels. At higher levels of organisation, factors including individual physiological tolerances, oceanography, species ecology and biology, and resource availability can all influence measures that could logistically be tested. Across all levels of organisation, special consideration should be given to whether the measure being tested is relevant to the research question at hand. These considerations include, but are not limited to, species ecology and biology, ontogenetic stage, body size, experimental acclimation times, environmental acclimatisation and intra- and inter-annual variability.

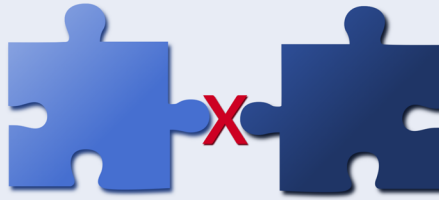
		INDIVIDUAL						POPULAT'N			COMMUNITY												
		Von Bertalanffy type growth models [A-C]						Individual-based Model (IBM) [P, Q]			Process-based/mechanistic SDMs [T]												
		Biphasic growth [D, E]						Physiologically structured population [R, S]			Cohort(individual) model [U, V]												
		Optimal allocation [F]						Process-based/mechanistic SDMs [L, N]			Age-structured end-to-end [W, X]												
		Dynamic Energy Budgets [G, H]									Size spectrum [Y, Z]												
		Aerobic Scope [I, J]									Models of intermediate complexity [AA]												
		Process-based/mechanistic SDMs [K-O]																					
INDIVIDUAL	PROCESS CATEGORY	PROCESS																					
	Physiological Capacity	Aerobic Capacity																					
		Bioenergetics																					
		Anaerobic capacity																					
		Immune capacity																					
		Sensory physiology																					
		Growth capacity																					
		Locomotor performance																					
	Behaviour	Behavioural response																					
	Plasticity	Phenotypic plasticity																					
	Reproduction and dispersal	Maturation																					
POPULATION		Fecundity																					
		Offspring condition																					
		Reproduction cost																					
		Reserve dynamics																					
POPULATION	Reproduction and dispersal	Recruitment																					
		Larval dispersal																					
		Movement																					
		Migration																					
		Habitat availability																					
	Biotic interactions	Density-dependent interactions																					
COMMUNITY	Adaptation	Genetic adaptation																					
	Human interactions	Commercial or rec. fishing																					
		Species introductions																					
		Pollution/habitat modification																					
Biotic interactions	Inter-specific competition																						
	Predator-prey interaction																						

Figure 2. Processes that are potentially informative for species redistribution studies (identified in Table 1) and their representation in a selected example of commonly used physiologically structured individual, population and community models. Shaded boxes indicate that the given process is represented explicitly (dark grey) or can be included implicitly (light grey), while white boxes indicate that the processes cannot be or are rarely represented. For individual models, community level processes cannot be included even implicitly, which is demonstrated with absence of boxes. For model descriptions (alphabetic notations) please see Supplementary material Appendix 2. Colour of process category indicates a match to Fig. 1.

(a) The problem: two pieces of the puzzle that do not fit together.

Focussed on observations

1. Shifting species
2. Experiments
3. Data
4. Model?



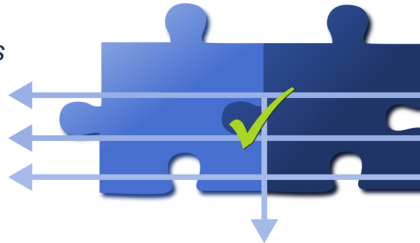
Focussed on modelling

1. Shifting species
2. Model
3. Process
4. Data?

(b) The solution: early dialogue with consideration of both observation and modelling perspectives.

Focussed on observations

1. Shifting species
2. Important processes?
3. Data needed?



Focussed on modelling

1. Shifting species
2. Important processes?
3. Models needed?

4. Integrating data and models

(c) The mechanics: an integrated framework to use.

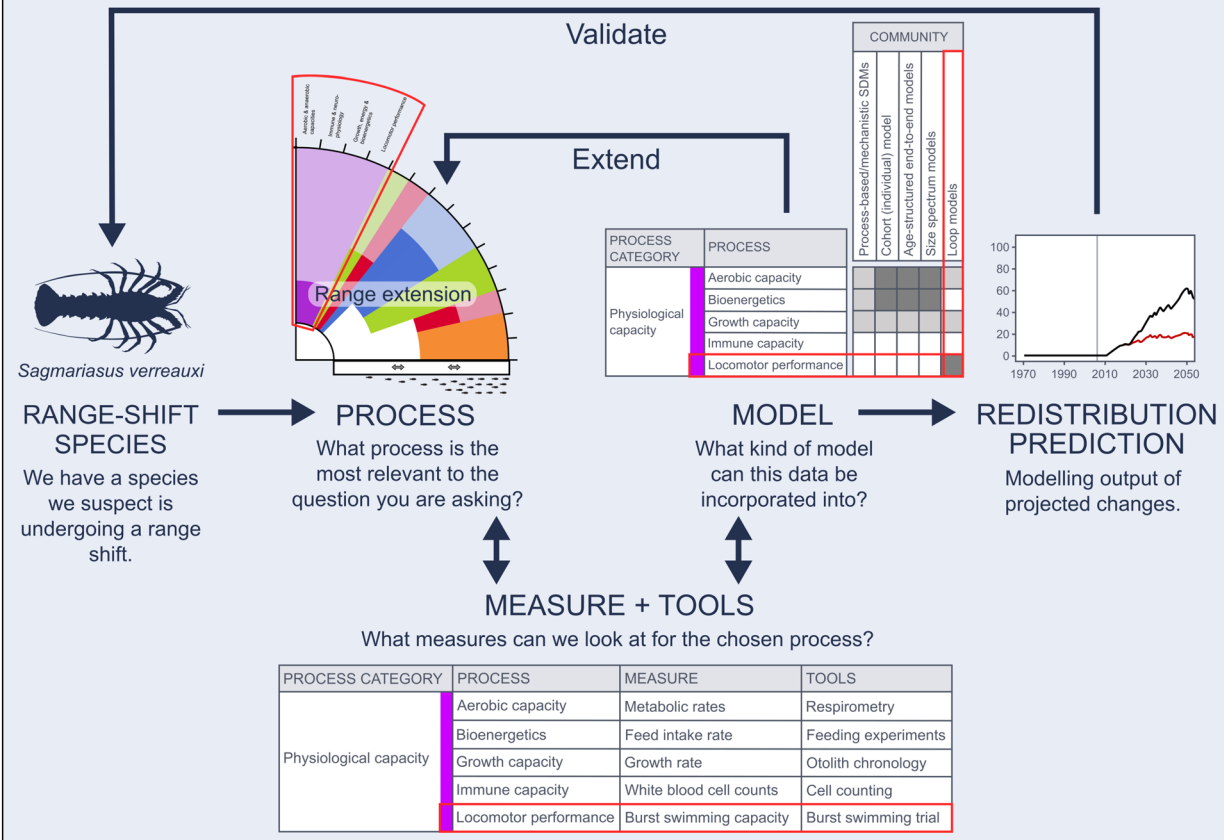


Figure 3. An example of the general lack of communication between different fields (a), and how better dialogue can improve the process of investigating species redistributions (b), via the use of the proposed framework (c).

An example of applying the above framework (Fig. 3c) was developed using the eastern rock lobster *Sagmariasus verreauxi*, which is a marine species suspected of undergoing a range extension in south-east Australia (Robinson et al. 2015, Twiname et al. 2019). We want to understand how this range extension will affect this species, and the existing lobster species within the area it is moving into, the southern rock lobster *Jasus edwardsii*. A first step would be to identify an important process (Fig. 1), e.g. locomotor performance to final larval stage (puerulus) of *S. verreauxi*. We want to know if pueruli can escape a predator in a new or changed environment. This is an important survival measure and ecologically relevant to this life stage. From the 'Measures and Tools' table (Table 1), we can investigate maximum speeds using a burst swimming trial and also see that locomotor performance can be included in a modelling approach that still accounts for species interactions (MICE models, Fig. 2). By experimentally investigating the effects of temperature on escape speed of *S. verreauxi* pueruli, and including this data in the loop model, it can be determined how this ecologically important process may affect the survival of *S. verreauxi* pueruli, and their potential range extension into a new area.

One very important thing to note is that using this framework can, and should be, iterative and adaptive (Fig. 3c). Was the predictive performance of the model good enough given the available data? If not, the dialogue about the important processes, data requirements and model suitability needs to continue. What new data could be quickly and easily obtained and included? Each iteration or adaption or addition to the data or the model will increase the knowledge of the species and/or system, and therefore the overall the robustness of species redistribution projection.

Discussion

Key challenges for better integration of species redistribution approaches between research fields

A major challenge in species redistribution ecology, is that, similarly to other interdisciplinary fields, opportunity for communication and knowledge exchange between researchers from different disciplines (or between those who use different methodological approaches) is limited. This disconnect also applies between ecosystems, for example between marine and terrestrial researchers. As a result, new knowledge and techniques are often not widely shared and assimilated. Future development in this field would benefit greatly from improved communication across methods and disciplines, to catalyse and integrate new knowledge and produce new strategies for furthering our understanding of species redistributions (McDonald et al. 2018, Kelly et al. 2019).

Selection of appropriate traits

One of the major challenges in predicting redistribution of marine ectotherms is the selection of appropriate traits that

drive species responses to climate change. Ideally, the value of individual traits are ground-proofed through correlation to an important performance measure relevant to the species' life stage. Fundamental processes, including growth, aerobic scope, survival or reproductive output, have previously been suggested as suitable unifying measures to predict overall performance (Clark et al. 2013, Fitzgibbon et al. 2017). Yet the question remains, whether species fitness can be appropriately represented by a single unifying trait, or if it requires multiple overlapping performance traits that vary with thermal history, between life stages (Fig. 4), within populations, and/or inversely with each other due to trade-offs (Chuang and Peterson 2016, Lancaster et al. 2017, Marshall et al. 2020). Currently, there does not seem to be an 'easy' solution to identifying singular or even several key traits that determine species performance, particularly as the importance of these traits is influenced and informed from different disciplinary perspectives. Ideally, analysis or experimental designs on multiple traits would include different process categories and organisational levels (Fig. 1). However, limited project time, as well logistical and financial constraints, mean this is most often not the reality. Reducing data collection efforts to key species (Bremner 2008), and the application of standardised methods to reduce methodological variation (Brown et al. 2016), may unlock the much needed capacity to investigate multiple traits and factors simultaneously and enable better identification of traits of key importance.

The selection of appropriate fitness traits must be guided by their ecological relevance and should be justified based on the species or life stage challenges and predicted measures of fitness. For instance, aerobic scope may be an insufficient predictor for animals facing frequent anoxic/hypoxic conditions such as crucian carp *Carassius carassius* or coral-dwelling gobies (*Gobiodon* spp.) (Nilsson and Östlund-Nilsson 2008, Sørensen et al. 2014). Other factors such as feed intake capacity (Fitzgibbon et al. 2017), olfactory predator sensing (Dixon et al. 2010) or predatory escape potential (Twiname et al. 2019) may be more appropriate for predicting performance and overall survivability of other species or particular life stages. Importantly, fitness varies among individuals and populations and is key to providing adaptive opportunity to select for phenotypes better suited under novel conditions (Eliason et al. 2011, Stitt et al. 2013, Moran et al. 2016). Therefore, assessing and reporting intraspecific variance or phenotypic plasticity in addition to mean fitness will be crucial to improve predictions (Donelson et al. 2012). Furthermore, the impact and type of relevant fitness traits may vary between life stages and be influenced by individual thermal history (e.g. acclimation, extreme events (Buckley and Huey 2016, Gunderson and Stillman 2015)) and interactions with other abiotic and biotic factors (e.g. Hypoxia, CO₂, competition (Pörtner 2012)).

The Oxygen and Capacity Limited Thermal Tolerance (OCLTT) hypothesis proposes that an ectothermic animal's capacity to perform aerobically, expressed as aerobic scope (maximum minus minimal oxygen consumption rate), is

a unifying proxy for whole organism fitness (Pörtner and Knust 2007). Following from this proxy, many distribution or performance models have been built on the assumption that higher temperatures will lead to oxygen limitation in marine ectotherms and that large individuals are more likely to be affected (Cheung et al. 2012, Pauly and Cheung 2018). While this is a mechanistic framework, increasing evidence conflicts with the general applicability of the concept (Clark et al. 2013, Jutfelt et al. 2018). First, the assumption of oxygen limitation goes against the principles of physiology, which states that under normal conditions (i.e. normal activity levels, non-extreme environments) organisms have ample ways to increase their oxygen uptake, so that the uptake reflects need rather than the converse (Lefevre 2016, Lefevre et al. 2017). When it comes to the aerobic scope, as a single measure of performance, new evidence shows that some species demonstrate aerobic scope increasing with temperature until death, and that other fitness related measures, such as growth, are optimised at different temperatures than aerobic scope (Clark et al. 2013, Norin et al. 2014, Verberk et al. 2016, Fitzgibbon et al. 2017, Twiname et al. 2019). Even in models based on the OCLTT, fitness is predicted to be optimised at a lower temperature than aerobic scope due to ecological and life history trade-offs (Holt and Jørgensen 2015). Thus, caution is required if selecting single fitness traits for new species and conditions, or multi-trait approaches without consideration of trade-offs. Various performance traits have co-evolved under selective pressure and physiological constraints and thus are linked by behavioural and life history trade-offs (Stearns 1989, Jørgensen et al. 2016). For example, predation risk increasing with foraging rate necessitates balancing survival and energy acquisition (McNamara and Houston 1986, Lankford et al. 2001) and a finite energy

budget requires trade-offs between fitness-linked performances (Lankford et al. 2001). A consideration of trade-offs is especially important in the context of climate-driven species redistributions. Climate stress is likely to directly affect life history trade-offs, especially at the leading and trailing edges of range shifts, where species are experiencing novel environments and novel selection pressures (Burton et al. 2010, Holt and Jørgensen 2014, Lancaster et al. 2017).

Careful selection of appropriate traits and the associated trade-offs is even more critical if they are to be integrated into existing mechanistic modelling frameworks. Apart from some of the physiological processes and debates described above, geneticists might see epigenetic control of temperature tolerance as of prime importance here, given that temperatures during the parental life stage seem to determine performance of offspring (Donelson et al. 2012). In contrast, evolutionary biologists might point out that the key question is about local adaptation among populations, given that populations adapted to different temperatures have different temperature-adjusted metabolic rates and sometimes can completely compensate for the effect of lower or higher temperatures on growth rates (Conover et al. 2009, Baumann and Conover 2011). Clearly, the species redistribution research community is still identifying key processes driving organisms' responses to temperature and other associated abiotic variables, and strong cross-disciplinary communication and exchange is key to success. In this regards our review of key traits aims to provide some much-needed direction, i.e. which of the traits identified in the Table 1 are the key drivers of species range shifts? And which trade-offs limit the range of values that a trait can take? The inclusion of all traits into mechanistic models would require thousands of parameters and long computation time, rendering models intractable.

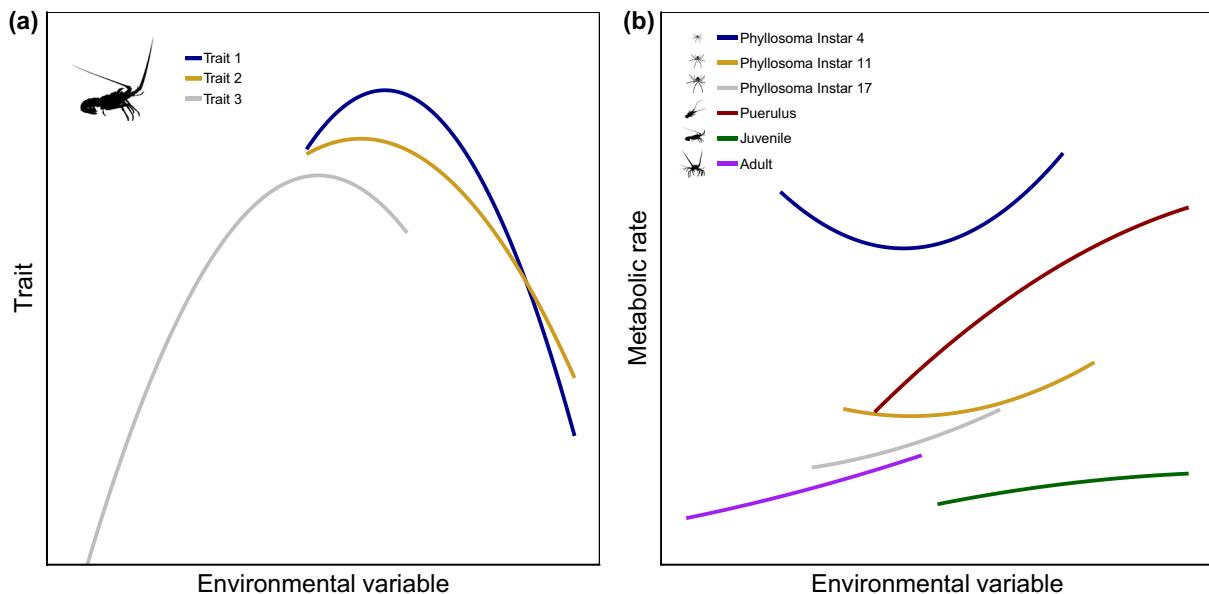


Figure 4. Occurrence of variable thermal performance curves of eastern rock lobster *Sagmariasus verreauxi*, depending on (a) the type of species trait or (b) life stage (Fitzgibbon et al. 2017, Twiname et al. 2019).

Yet, the potential exclusion of essential trade-offs would result in unrealistic model dynamics, e.g. creating ‘super-species’ that would prey on everything and spread anywhere.

Modelling challenges

Assuming that the key traits and trade-offs to be included in mechanistic models have been identified and agreed upon, the next challenge is in establishing whether the model predictions are accurate, given the available data. One important development required to assess the validity and predictive power of new models is an improved uncertainty evaluation. If models provide only a single outcome, given one set of selected parameters, it is difficult to ascertain the range of uncertainty and conditions under which this prediction is likely to apply. It is therefore also difficult to validate model predictions with empirical data, i.e. how similar the predicted and observed datapoints should be for us to accept the model predictions? Physiologically structured models, especially more complex ones applied at community level, typically lack broadly accepted statistical uncertainty evaluation, and this is an important limitation to acknowledge when such models are applied to inform management and conservation decisions (Spence et al. 2015, Morzaria-Luna et al. 2018). Recent developments in computing power and statistical methods, are however increasing the feasibility of uncertainty evaluation of complex models, so we can expect and, in fact, demand, improvement in this field over the next decade.

A fundamental challenge in using physiologically structured multispecies models to understand and predict species redistributions, is to ensure that performance and abundance of species in the model emerges from environmental processes and species interactions and is not inadvertently hardwired in the model assumptions. Multispecies models usually require some form of parameter calibration to identify parameters that allow species coexistence (Andersen et al. 2016). Adding new species into a model requires its parameters to be specified, but the specification can determine success of a new species in the modelled community, rather than allowing it to emerge dynamically. This is a critical question that requires careful assessment and collaboration within the modelling community. Spatially-explicit or geographically-coupled models, could in principle overcome this challenge; ecosystem models, such as Madingley or Atlantis (Fig. 2; Supplementary material Appendix 2) include migration and can allow for dynamically emerging changes in species composition in different cells of the model, if the cells have different environmental conditions and the environmental tolerances are included (Harfoot et al. 2014, Audzijonyte et al. 2019). However, these models still require parameters that will determine when and how a species should move across model cells and more research is urgently needed to better specify these conditions.

The primary challenge for modelling species redistributions with mechanistic models is that most of these models generally have not been developed to explore questions of range shifts and, therefore, inherently make a historical assumption

that species composition remains stable. As species range shifts accelerate (Parmesan and Yohe 2003, Chen et al. 2011, Poloczanska et al. 2013, Lenoir et al. 2019), the assumption of fixed species composition will become increasingly weak. It is now imperative for the research community to find practical and transparent ways to combine lessons learned and expertise gained through the historical development of physiologically structured models with contemporary species redistribution research. The coupling of correlative and mechanistic SDMs has been proposed as one way to proceed; for example, as applied at a community-level to terrestrial systems (Mokany and Ferrier 2011). While coupled approaches are a crucial step towards a mechanistic understanding of species redistribution, and could be expanded into the marine realm, these approaches still remain grounded in correlative relationships between species occurrence or abundance and present-day environmental conditions. The development of mostly mechanistic tools is an important step towards better understanding and eventually predicting how species will respond to novel environmental conditions that are outside the climate envelope under which correlative relationships have been developed. This will be a challenging but a big improvement towards projecting climate-driven species redistributions, where species responses to environmental change emerge dynamically in response to the underlying processes.

Data availability

The capacity to undertake primary scientific research underpins the development of mechanistic understanding of climate-driven species redistribution. For example, implementation of the tools suggested in Table 1 is necessary for quantifying key species performance measures under climate change scenarios, which can then be applied to design, improve or parameterise predictive models for understanding broader ecological response to global change. Despite the rapid marine climate change that is affecting coastal ecosystems in developing countries (Hobday and Pecl 2014), researchers in these areas are unlikely to have access to equivalent resources as researchers in developed countries. Thus, it is greatly important to explicitly consider the financial and resource limitations associated with implementing methods for improving our mechanistic understanding of species redistribution within these contexts, and prioritising approaches that can optimise the ratio between research costs and benefits is a key for progress. For instance, measuring responses from species that are of key ecological and/or economic importance to environmental variables strongly affected by climate change (e.g. temperature and dissolved oxygen) will likely be of primary significance and should be a focus priority. When additional data are required to inform broader population, community and ecosystem level analyses, systematic literature reviews may facilitate a robust estimation of the required parameters. Additionally, knowledge sharing among researchers studying the effects of climate change on geographically disparate, but similarly affected regions of the global ocean can help to address the financial and resource

limitations that constrain ecological research in developing countries. For example, the Marine Hotspots Network (<www.marinehotspots.org>) aims to document and communicate climate-induced ecological change from a variety of rapidly warming marine regions in order to improve the capacity of similarly affected, but under-resourced, regions to understand and adapt to the effects of climate change.

Future directions

The use of mechanistic species distribution or ecological models is often discouraged based on their seemingly impossibly large data requirements. Certainly, measuring each performance trait for every species in the world under strict experimental conditions will be impossible. However, we do need to make the best use of theoretical and technological advances and continue to develop them. On one hand, we can use general macro-physiology or energy budget principles that set limits on the range of possible parameter combinations and allow extrapolation across species (Brown et al. 2004, Kooijman 2010, Dell et al. 2011, Pawar et al. 2012). On the other hand, technological advances, such as animal borne sensors, machine learning and automatic underwater vehicles can potentially provide large sets of data for specific species (and improve the general principles in the process). Evans et al. (2016) provides potential solutions to some of the barriers of using mechanistic models, including data availability. Perhaps we should not only design research tools or develop models based on data we already have (although this is inevitably needed), but instead identify the knowledge and data needed to understand processes that influence species range shifts (Evans et al. 2013, Wolfe et al. 2020). The models that could be developed from such an approach could then advise the collection of new data critical to continuing the improvement of understanding of the drivers behind species range shifts. Additionally, our general knowledge and understanding of climate-related range shifts may also be improved by addressing taxonomic and geographic knowledge gaps relating to research on climate-related range shifts, e.g. as highlighted in Lenoir and Svenning (2015).

Some of the major questions related to species range shift understanding and predictions that could be resolved by increased interdisciplinary collaboration include.

1) Predator–prey interactions and competition: how could laboratory or telemetric sensor-based measurements of activity levels (heart rate, swimming speed, etc.) be used to better inform feeding rates and vulnerability to predation in mechanistic models?

2) Immune physiology: how can immune response measurements in the lab be used to parameterise non-predatory mortality in mechanistic models?

3. Genetic adaptation: how can multi-generational experimental data and genetic studies on local adaptations be incorporated into long-term model predictions to account for adaptation to changing conditions? If spatial gradient studies demonstrate that populations in warmer conditions have

higher tolerance to temperature, should model responses be scaled down through time and, if so, how rapid should these responses be?

4) Aerobic capacity: how can experiments on aerobic capacity be used to scale physiological processes in mechanistic models, considering that models deal with multi-generational timescale? Which processes are best informed by the aerobic capacity measures, and are acute experiment findings relevant for modelling long-term responses?

5) Recruitment: what is a rigorous and generally accepted way to include ‘stock–recruitment’ and other early density dependence relationships and how are these likely to be affected by climate and species redistributions? Which proxies could be used to assess changes in recruitment, and under which conditions could regime shifts be expected (which would make models unreliable)?

Conclusion

Scientific evidence suggests that we are currently experiencing the largest climate-driven global redistribution of species since the Last Glacial Maximum, 20 000 yr ago (Scheffers et al. 2016). We must urgently collaborate around these and other questions to improve our shared understanding of the complex suite of processes underpinning climate-driven responses, to provide the best possible support for adaptation efforts, now and into the future. This progress must be fast – with structured approaches to co-designing research as outlined here, with data and models fit for joint purpose.

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Supplementary material (available online as Appendix ecog-04996 at <www.ecography.org/appendix/ecog-04996>). Appendix 1–2.